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THE SYSTEM OF THE ORDER GEOPHILA (HELICIDA) (GASTROPODA PULMONATA)

## MORPHOLOGY, SYSTEMATICS AND PHYLOGENY OF MOLLUSKS



# THE SYSTEM OF THE ORDER GEOPHILA (=HELICIDA) (GASTROPODA PULMONATA)

by

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Generally speaking the fewer the characteristics employed as bases for the systematics of any group of animals, the more consistently harmonious that taxonomic scheme seems to be. When using numerous characteristics relating to particular organs or structures, one often elaborates a less harmonious, though more synthetic, system because certain groups of features fail to correspond to others. Also the more adequate system is strengthened by the utilization of a holistic approach wherein the various morphological systems are viewed as inter-related parts of an organic whole, the result of the dynamic forces of evolution. At higher taxonomic ranks, the indicators of evolutionary and developmental pathways of the various organs and structures take on greater significance.

Turning our attention to the current systematics of the Order Geophila, we recognize that attempts to understand their phyletic relationships have fallen short of a holistic analysis. Reduction of, and substitution for, one organ by another has been frequent while problems of parallelism and convergence have often been insufficiently appreciated. Only through a more thorough analysis of such phenomena, including a study of variation between species and among genera as well as the discernment of evolutionary pathways will a more comprehensive, phyletically accurate system emerge.

Various opinions of the systematics of the order exist. Most specialists accept the one proposed by Pilsbry (1900) which is based

on the characteristics of the structure of the excretory apparatus; and he divides the order into 3 suborders: Orthurethra, Heterurethra,<sup>(1)</sup> and Sigmurethra. Later a fourth group, Mesurethra, was added by Boettger (1954) who shared Pilsbry's opinions. Solem (1959) proposed a phylogenetic system based on the unconnected branches Orthurethra, Sigmurethra, Mesurethra, and Tracheopulmonata plus Heterurethra. Thiele's system (1931), based primarily on conchological features, has often been subjected to criticism from the point of view of the anatomist, although the validity of many of Thiele's formerly rejected arguments should now be recognized. The system proposed by Wenz & Zilch (Zilch, 1959-1960) is a compilation in which Thiele's system, modified to conform to newly accumulated facts (between 1934 and 1959), was superimposed on Pilsbry's earlier scheme. The most widely currently accepted arrangement is the one proposed by Taylor & Sohl (1962), where the same suborders appear, divided into 19 superfamilies.

Moreover, the largest group, Sigmurethra, was divided by H.B. Baker, following Pilsbry, into the infraorders, Holopoda and Aulacopoda, plus a new infraorder, Holopodopes. The members of these groups are distinguished by the nature of furrows or grooves in the foot. In Holopoda and Holopodopes

(1) Heterurethra as understood by Pilsbry includes 3 independent groups (accorded ordinal rank by Soviet malacologists): Succineida, Aylliida, Athoracophorida (Minichev, 1971; Minichev & Starobogatov, 1975; Slavoshevskaya, 1971; Van Mol, 1967). For this reason the early groups of Heterurethra will not be treated here.



the peripedal furrow runs along the margin of the sole or slightly above it, the sole itself always being entire. In Aulacopoda the peripedal furrow is placed noticeably higher than the margin of the sole and the sole itself is often divided by 2 parallel furrows. The obstacle to uniting Holopodops and Holopoda lies in the fact that Baker assigns them to different phylogenetic branches: the first is lower than Sigmurethra, the second is higher.

Hence up to the present, three groups of characteristics have been proposed as suitable bases for the construction of a system for the order Geophila: conchological, excretory, and pedal. In addition, the sexual apparatus has been used in diagnosis at the familial or generic levels. We plan to examine separately a series of groups of characteristics; to simplify matters, we will limit ourselves to the discussion only of the system which we here propose.

We are certain that those of our colleagues who are also interested in the systematics of the Geophila will offer corrections on the basis of new facts: nevertheless, the author is convinced of the validity of the basic classification here offered.

## THE SHELL

It is commonly admitted that conchological features in general possess only little taxonomic value and that the area of their application is limited to the familial level, and more often to the generic or specific levels. Though partly true, there are some shell features which possess a considerably greater informative value which permits their use at higher taxonomic ranks. The general appearance of the shell, as well as the presence of longitudinal parietal and columellar plates, are such characteristics. Naturally, when we speak of the general shell shape, we do not include the numerous secondary modifications.

The first problem to present itself in our investigation concerned the nature of the original Geophila shell. If we assume that the order derived from ellobiid-like ancestors--both fossil and Recent Ellobiidae are characterized more or less by a monotypic shell of elongated form with columellar and parietal plates--then we must accept such a shell type as the original shape. This almost universally accepted opinion is reinforced by the fact that the ancient (and although, in our opinion, only distantly related) Partulidae and Achatinellidae do indeed possess precisely such a kind of shell; in fact, that shape is characteristic for the lower Orthurethra as well as for the lower non-orthurethrous Geophila. At first glance, serious deviations from this shell type among the lower Geophila are seen in Pupilloidea and Sagdoidea: i.e. the Pyramidulidae, Valloniidae, Strobilopsidae, Sagdidae, and Thysanophoridae. However, the microhelicoid shells, characteristic for the families cited, are "inscribed" in the beginning as bulimuloid shells, which, in combination with anatomical features, give testimony to the origin of those families by means of the early sexual maturity of the ancestral form,

and consequently in the early interruption of shell growth. The appearance protandry (e.g. in the Valloniidae), which leads to the swift reduction of the male genital system after having performed its function, is another consequence of the change of the bulimuloid shell to the microhelicoid.

In the almost limitless variations of the shell of the Geophila, one can detect several evolutionary lines. To complete the survey of the lower members of the order, we note a tendency toward reduction of the parameters and retention of the same proportions (e.g. Pupillidae, Cionellidae, Vertiginidae, and Orculidae). This tendency is bound up with life in microhabitats, often--but by no means always--in climatic conditions of sharp daily temperature changes.

The other tendencies fit in with the natural groupings, that is, with the suborders proposed in the present work. Thus high, many-whorled shells, characteristic of most of the Achatinidae may reach a very large size in a moist tropical climate. The inhabitants of forest, and secondarily of mountains, often crawl on vertical surfaces and frequently with the ventral side upward and evolved a long narrow shell shape (Clausilioidea). The columellar plates in such cases may grow stronger since they are the point of support for the columellar muscle and they facilitate the evolutionary direction of shell shape (Likharev, 1962).

In the lower Oleacinina, the shell initially is of the same type, but members of this suborder inhabit a large number of biotypes and this explains the heterogeneity of their shells. The greatest degree of this is seen in the Streptaxidae, among which can be found almost all types of shell shape seen in the Geophila (Zilch, 1961), and above all, in the unique shell type of Gonaxis with its displaced or distorted axis. The Oleacinidae possess several unique shell features, rarely encountered elsewhere than in the suborder

Oleacinina: the aperture is high and narrowed in its upper angular part and is not expanded laterally: the combination of such an aperture with strongly flattened whorls and weak sutures gives the shell a bullet-like shape, thus enabling the animals to crawl in the soil in their hunt for oligochetes, their basic food. The angular area of the apertural region is an adaptive feature: in this region the pneumostome is displaced and the mollusk can breathe freely while the anterior part of the body is buried under the solid surface. Characteristically, a similar shell is encountered in those members of other suborders which are also closely bound up with the soil. It is enough to observe that a predatory life style in the Oleacinina brings about a tendency to shell reduction as in the case of two other higher suborders, the Helixina and the Limaxina. (1)

Shell reduction itself proceeds along two evolutionary pathways associated with either 1) the widening of the last whorl and consequently of the aperture, or 2) the increasing of the relative height of the aperture. The reduction of the shell may proceed either through a regularly whorled spiral of the shell or a regular reduction of the spire. In the Helixina the attainment of the slug shape proceeds along the first path: this process can in detail be followed in the Vitrimoidea. Among the Oleacinina, the Testacellidae, however, lose their shells by passing through a "succinoid" stage. The increase of the relative apertural height can be traced in some New World Oleacinidae: Euglandina flammulata H.B.B.--Pittieria arborea H.B.B.--Euglandina pupa H.B.B.--E. delicatula (Shuttl.) -- E. saxatilis H.B.B.-- Oleacina camerata H.B.B. (Baker, 1941) -- Strebelia berendti (Pfr.). In the first few of these species the aperture height is 35 o/o of the shell height, in the last it is 93 o/o; that is, the aperture is barely shorter than the shell.

(1) To distinguish them from the generic names Helicina and Limacina.

Similarly in the lower suborders (Achatinina, Oleacinina, and Pupillina, together with a high shell, there is also the presence of columellar plates which may either disappear or grow stronger and more involved. The truncated columella in the Oleacinidae, Cionellidae, and many Achatinellidae, etc. comes about as the result of the reduction of the lower part of the columella below the plates: the lower columellar margin in this case corresponds precisely to the columellar plates.

The apertural plates mentioned above consist of contrasting basal and palatal elements. The fact is that these two groups of apertural formations have a different historical nature, different taxonomic importance, and different functions.

As far as the basal and palatal folds are concerned, they repeatedly and independently originated in all the suborders which are themselves characterized by a large degree of diversity and variability even within individual species. Their role in the final analysis is related to the narrowing of the opening of the aperture. Their beginning is bound up with the narrowing of the last whorl before they reach their definitive state. As a result of this narrowing the secretory surface of the mantle is reduced by folding, and the formation of the folds leads to the origin of the apertural armature.

A greatly complicated matter is seen in the columellar and parietal elements. We emphasize the fact that there is no important distinction between them: in many ellobiids the boundary between the columellar and parietal apertural margins is indistinct and there are not one but many columellar platelets (appearing, apparently, as a result of the fracturing of one of them) by which the upper columellar plates actually rest on the parietal wall. In contrast to the basal-palatal formations, originating either at the very end of postembryogenesis, or several times in the course of the life of the mollusk

(Schileyko, 1967), the columellar parietal plates appear even in embryogenesis and continue to lengthen as the shell grows. Apropos the origin of the plates, it may be thought that the single origin of the plates is a consequence of the heterogeneity of the ellobiid ancestral shell. Such heterogeneity is actually present in some ellobiids. It is understood that because of the "break" in the columella at the junction of the embryonic and definitive whorls, an oblique fold appears, which extends, as the shell is growing, to the aperture.

The special function of the columellar plates apparently consists in serving as a support for the columellar muscle. In cross section it is seen that this muscle rests on the upper surface of the plate: if there are 2 plates, the muscle lies between them; when there are more than 2 the muscle breaks up early into branches, each of which occupies a niche between 2 neighboring folds. The latter condition can be seen, for instance, in the Urocoptidae which have relatively small bodies and thus the problem of the narrow shell is especially severe. Under such conditions the columellar muscle allows the shell to continue to grow in the set direction.

The principle role of the parietal plate is to force itself into the mantle cavity and incompletely divide it into right and left halves. We recall that the vascularization of the right and left halves of the lung is different: the respiratory inflow first enters the left half of the cavity and leaves it through the right: thus the character of the gas exchange along the entire plane is not equal. Apparently the more primitive division of the pulmonary cavity was brought about to regulate the air current and to increase the effectiveness of breathing -- a creation of the incompletely formed partitions. Later such a method of dividing the lung gave way to a more perfect, active, and sensitive method with the help of the mantle folds

in aquatic Basommatophora (Sullivan & Cheng, 1974), the Helixina, the Limaxina and thus, independently, in the remaining higher suborders of the Geophila.

In contrast to the Achatinina, Oleacinina, and Pupillina, the shell of the Helixina and Limaxina was originally depressed and had a wide umbilicus as often found in the Geophila. However, a wide umbilicus is not a peculiar phenomenon among the Geophila; it usually is not seen in mollusks with a shell diameter of more than 1 cm, and animals with such a shell live in strongly shaded areas. In similarly shaped shells the relative area of the surface is large and its usable volume is small with a large umbilicus (Fig. 1A). While as the umbilicus narrowed, the volume which was taken up by the columellar cavity was "given over" to the accommodation of the internal organs (Fig. 1B). The usual mode for the narrowing of the umbilicus was through the widening of the whorls; at times only the body whorl grew wider and thus the interior of the shell remained a cavity in communication with the interior narrow umbilical aperture.

The columellar parietal plates in some African and Pacific Endodontidae are not homologous to those of the Achatinina, Oleacinina, and Pupillina which are formed at the end of post-embryogenesis; they may originate convergently.

Many Helixina possess thick-walled, trochid-shaped or spherical shells of a helicoid appearance without any apertural armature; however, in such cases, when the apertural teeth are present, the area in which they appear is limited to the aperture and the adjacent section of the parietal wall: they do not run along the columella or the parietal walls to any distance

inside the shell. Further in this suborder there exists a tendency to a thinning of the shell, and the repeated appearance, within the suborder, of the slug form.



## THE RENOPERICARDIAL COMPLEX

We have already discussed the data and elaborated on the taxonomic and evolutionary significance of the renopericardial complex (Schileyko, 1976 a; see also Minichev & Starobogatov, 1971). We will therefore here discuss only the basic proposals.

In embryogenesis at a stage comparable to the veliger, *signaturethry* is a feature even in orthurethral forms with both having the urethras as open furrows. Basically in the Orthurethra the kidney differs from the kidney of related Geophila only because of its greater length. In the more progressive groups the processes of the shortening of the kidney and the closing of the urethra take place as an evolutionary parallelism that is not necessarily synchronous. The suborder Pupillina as here proposed, differs from the Orthurethra only in excluding the Partulidae and including the Sagdoidea. In other words, the Orthurethra is basically a natural taxon but contrasting it with other entities at the same rank on the basis of the excretory apparatus is not justified.

The Heterurethra evolved as a result of the decrease of shell size and the consequent shortening and widening of the lung. Here the kidney turns either clockwise or counter-clockwise and squeezes itself into the posterior wall of the mantle cavity, finally becoming buried inside the visceral sac.

In these ways the features of the renopericardial complex offer good data for reconstructing the phylogenetic relationships in superfamilies, families, and sometimes genera, but they are not suitable as basic characteristics for suborders.

## THE PEDAL INCISIONS

The positions of the longitudinal grooves in the foot are used for the classification of only the higher Geophila -- the Sigmurethra. If one takes the order as a whole, then in the Achatinina, Oleacinina, and the majority of Pupillina the foot is of the holopod type and only in some Helixina and Limaxina is it aulacopod.

In the present article we designate the furrows running along the sole as the pedal furrows, those running along the edge of the sole as peripodal furrows, and those on the lateral surface as suprapodal furrows.

What is the function of the furrows? The pedal furrows, seemingly facilitate the intensification of movement by strengthening the functional loading of weight on the central field of the foot; waves of muscular contraction in this case move along the central field. The peripodal and suprapodal furrows are channels along which, with the aid of a ciliary epithelium, mucus is driven and thus they perform varied protective functions. It is natural that such furrows are formed as a result of life in arid conditions, and, in the ancestral aquatic shape, permanent furrows were absent in the foot. The first furrows which appeared in the dry-land forms were small longitudinal ripples, issuing from below the buccal flap and reaching the anterior half of the body (e.g. Partulidae, Fig. 2, I, II). Later one of these is fractured into a ring-shaped peripodal furrow, occupying an extremely lateral position (e.g. Ceriidae, Subulinidae, Clausiliidae, Pupillina (Partly), Helixina (Fig. 2, III) or a suprapodal furrow (Vitrea, Fig. 2, VIII). One at times may think that the suprapodal furrow is displaced and thus moves to an extreme marginal position (Fig. 2, from VIII to III).

The pedal furrows are usually homologous (in their derivation) to the primary suprapedal or peripedal furrows. The only exceptions are those very rare cases when a single medial pedal furrow appears (Zonitoides, Rhytida, Fig. 2, VI, VII) which originates in a fold in the foot caused when the animal draws itself into its shell and thus it becomes isolated (Schileyko, 1972a).

Historically the succeeding furrows often appear later than the first pair of peripedal furrows, and, as the first pair "slips down" to the sole, they occupy their place (Fig. 2, from III to IV to V and from VIII to IX to IV to V).

At the same time a second way leading to the origin of the tripartite division of the sole is conceivable: namely as a consequence of the increase of weight on the central part of the holopod sole. Thus, in crawling, Achatina the waves of contraction do not take in the whole surface of the sole (Fig. 2, X): the pedal branches of the columellar muscle are strengthened in the central field, and the lateral fields are moved in a vertical direction. In other words, a preadaptation to the formation of a tripartite sole (Fig.2, from X to XI) is apparent here.

Thus (because of convergence) the pedal incisions are not suitable for taxonomy on the level where they are most used. Even Pilsbry admitted this when he recalled instances where the members of the Aulacopoda had a holopod foot, and members of the Holopoda had an aulacopod foot (1946: 231-232).

One conclusion which could be drawn from the data is extremely important for a further discussion, namely: the holopod type of foot in any case will be the point of departure leading to the aulacopod. The latter

arises in those groups whose members are in need of rapid mobility: either predators or slugs upon whose speed of movement depends the success in the passive struggle against dessication.

## THE SEXUAL APPARATUS

The question regarding the appearance of the sexual apparatus in the Geophila is of prime importance. As long as we assume that the Orthurethra are the most primitive group, we must also assume the same for their sexual systems. But the sexual apparatus of the orthurethral Pupillina is specialized rather than archaic and cannot be regarded as the point of departure for the other types.

If we leave aside the numerous cases of secondary simplification, then the primary simple structure of the genitalia is found mostly in the primitive Achatinina and Helixina: in the first case the Partulidae and Strophocheilidae, in the second the Punctoidea (in the Pupillina and Oleacinina, the most primitive forms do indeed possess appendages in the male portion). Thus, the original type of the sexual system is extremely simple: from the albumen gland issues the spermoviduct (hermaphroditic duct) which then divides into two parts, of which one is the seminal conductor (vas deferens) which is longer than the vagina and forms a lateral loop. The spermatheca is still not differentiated into a channel (spermathecal duct) and reservoir (spermathecal sac) and is represented only by an elongated sac off the vagina.

The longest appendage, the flagellum, is formed in a basic way (Fig. 3). The first way is by moving the point where it enters into the seminal conductor (vas deferens) below the epiphallus. The second mode comes about by close contact of the distal part of the seminal conductor (vas deferens) to the penis and the subsequent disappearance of the partition between these channels. In general, it may be said that for the Pupillina and most Helixina the first way is characteristic while the second is for the Achatinina and

## Endodontinia.

In general, in the Achatinina, Endodontinia, and Limaxina the sexual apparatus is close to the original type. But in the superfamily Achatinoidea there is one peculiarity rarely seen in this suborder: the seminal conductor (vas deferens) is in close contact with the penis and epiphallus and often is joined to these channels, covered by a muscular connective tissue. In most Achatinina the cover is clearly seen in the lower part of the penis, and in this case the seminal conductor (vas deferens) pierces the said cover or passes below it (Araujo, 1973; Breure, 1974; Mead, 1950). Often -- and in various Helixina -- a penial sheath is formed, but here the seminal conductor (vas deferens) either remains free or is drawn to the atrial area by sheaves and does not penetrate its own cover.

If we now turn to the Pupillina we see the unique genitalia of this suborder sharply delineated. The penis has two appendages (Fig. 4): a small caecum and an appendix consisting of 5 sections. In a full view we distinguish: 1. a basal cylindrical, swollen section (A1); 2. a spherical section separated from the base by a sphincter (A2); 3. a short, narrow cylindrical structure (A3); 4. a thin tube with muscular walls (A4); 5. a widened, lengthened ampule (A5) (Schileyko, 1976b). Based on this -- and many authors, without providing data, homologize the penial appendix with the stylophora (dart sac) and mucus glands of the higher Geophila (Albers, 1860; Forcart, 1940; Ihering 1892; 1909; Wiegmann, 1900) -- we must note that the appendage fulfills a stimulating function before coitus. There is also the supposition that the appendage is involved in the reception of the partner's spermatophore. As to the caecum, Forcart (1940) ascribed to it the function of the mechanical place of the retention of the spermatophore before copulation.

The function of the epiphallus (and flagellum) is the same as in other groups with spermatophores; namely, the formation of a cover for the latter.

It's easy to understand the role of the caecum when an individual with the spermatophore still contained inside the penis is opened: the cover of the latter has a "spur" formed in the cavity of the caecum corresponding to the shape of the cavity. The spur apparently is an anchor which prevents the spermatophore from leaving the sexual system earlier than is necessary. The spermatophore itself has a gutter or furrow "over" which is drawn a thin film, but the film is absent in the posterior part (Fig. 5). In a histological examination of individuals of some Buliminidae species, collected immediately before copulation, sperm was detected inside A5. It is apparent that this could not be allosperm (sperm of the partner); firstly, because coitus had not yet taken place, and secondly, because there is a spermatheca for the reception of the allosperm. Consequently the sperm noted was autosperm and thus A5 serves as a supplementary depot for the autosperm where the latter enters before coitus and possibly there also awaits the period of ripening.

To sum up, in an animal ready for coitus the sperm is collected inside A5, and the spermatophore is formed already but it is empty. In copulation the penis is twisted, A1 and A2. The spermatophore is delivered to the partner, and when the larger part of it has already left the penis, the sperm is forced into the cavity of the spermatophore cover by contraction of the musculature in A3 and A4. A2 serves as the regulator of the entrance of sperm into the spermatophore since it is provided with one or two sphincters and papillae.

This is the situation in many Palearctic Pupillina. Extraordinarily

interesting modifications of this type of genitalia appear in the Pacific Achatinellidae (Cooke & Kondo, 1960): in members of some groups there is a substitution of the penial appendix, as a result of which the latter is reduced.

To account for this modification of the male apparatus among Pacific taxa, one expects to see some reduction of the penial appendix among Palearctic families. Indeed, there is only a single family where this occurs: the Orculidae (Schileyko, 1976b; Steenberg, 1925) -- which in any case shows a large degree of uniqueness in the organization of the male sexual structures.

Furthermore in the Geophila the presence of a more or less complicated structure of the quadrvia is characteristic, in the composition of which there is a fertilization chamber, a spermatheca and also incurrent and ex-current channels (L. Schileyko and A. Schileyko. 1975; Flasar, 1967; Lind, 1973; Van Mol, 1971). As far as is known, the only group where the quadrvia are represented simply by a bend of the hemaphroditic channel is the Partulidae, and this bears witness to the primitiveness of this group when compared to the other Geophila.

Once again we emphasize the fact that the simplest sexual apparatus as a whole is found in Achatinina (Fig. 6) and thus this simplicity is of a primary character. The most complicated element -- the penial papillae -- is only seen from time to time in this group (Fig. 6, V) independently of the formation of analogous structures in other suborders.

The sexual apparatus of the higher Helixina -- Helixinia and Zonitina and also Limaxina has an entirely different aspect. In these taxa the primary presence of vaginal appendages is characteristic -- the sarcobelum, stylophores or other appendages like the atrial gland in Milacidae. The most



commonly associated organs of the stylophores are the mucous glands although at times the sarcobelum is also provided with glands.

It may be thought that all these appendages came about as a result of a differentiation of non-specialized glandular tissue in the lower part of the vagina, since their formation took place no fewer than 3 times: 1) when the 4 stylophores and mucous glands are arranged like a wreath around the vagina (Humboldtianidae); 2) when the 4 stylophores are arranged in 2 rows (Hygromioidea); in both cases the number of stylophores is reduced to one; 3) the position of a single sarcobelum.

As for the male portion in the Helixinia, in the Endodontinia the penis is simple, at times sac-like, often with internal appendages (Climo, 1969, 1970, 1971); Riedel and Wiktor, 1974; Solem, 1970). The only external appendage -- often absent -- is the flagellum. The penis of the Helixinia, especially in the Vitrinioidea, is more complex. Here, in addition to the flagellum, there is also a caecum, not homologous to the caecum of the Pupillina. In answer to the complicated shape of the spermatophore cover, the cavity of the flagellum is also complicated. In a series of Recent forms, one can trace the process of the simplification of the male portion through the disappearance of the caecum; the flagellum likewise shortens and may be reduced, and the surface of the spermatophore is often also simplified. In Pseudoaustenia (Ariophantidae) the flagellum also disappears, but the internal surface structures, characteristic of the species, have an internal epiphallus (Van Mol, 1973). Among various taxa of the Helixinia, as also among the Achatinina, the formation may be seen of a penial sheath (many Euconulidae, Helicoidea, Vitrinioidea, etc.).

Finally there is one other important element in the male portion -- the

penial papillae. Very often the papillae are present in the Helixinia, and in some cases even 2 papillae are formed (Schileyko, 1972b), but these may appear independently in members of all the other taxa.

In conclusion we note that there are no characteristics in the sexual apparatus sufficient to clearly differentiate 3 infraorders within the Helixinia, even if we do not consider the reduction of characteristics which may lead in time to a formal resemblance based on negative characteristics. Thus several Helicoidea (Oreohelicidae, Bradybaenidae) characteristically have one stylophore on which the mucous glands are located; however, on the external sarcobellum in Elaphroconcha (Ariophantidae), 4 mucous glands are similarly located.

We now proceed to the diagnostic characteristics of the suborders and the infraorders, and we will also attempt to define their limits and size.

Order Geophila Ferussac, 1812

Suborder Achatinina Schileyko, new

The shell is achatinoid, bulimuloid, or elongate-fusiform in shape with columellar lamellae. Longitudinal parietal lamellae are absent or present only in the last whorl; the aperture often lacks teeth. The sexual system is without appendages except for a flagellum on the penis; often there is a close connection of seminal duct (vas deferens) to the penis and a penial sheath appears. The kidney is shortened with the urethras closed to differing degrees. The foot is holopod. Obligatory predators are not found in the suborder. Oviparous, very rarely is ovoviviparity observed.

1. Superfamily Achatinoidea

(Megalobulimidae Leme, 1973, Strophocheilidae Thiele, 1926; Odontostomidae Pilsbry et Vanatta, 1898; Bulimulidae Tryon, 1867; Amphibulimidae Crosse et Fischer, 1873; Anadromidae Zilch, 1959; Achatinidae Swainson, 1840; Dorcasiidae Conolly, 1915; Acavidae Pilsbry, 1895; Clavatoridae Thiele, 1926).

2. Superfamily Subulinoidea

(Subulinidae, Crosse et Fischer, 1877; Ferussaciidae Bourguignat, 1883; Stenogyridae Wenz, 1923).

3. Superfamily Clausilioidea

(Megaspiridae Pilsbry, 1904; Urocoptidae Pilsbry et Vanatta, 1898; Clausiliidae Mörch, 1864; Filholiidae Wenz, 1923).

4. Superfamily Partuloidea

(Partulidae Pilsbry, 1900).

### Suborder Oleacinina Schileyko, new

For the most part the shell is elongate with columellar lamellae. Longitudinal parietal lamellae are wanting though the aperture at times has teeth. The female genitalia do not have appendages and in the male portion, the penis is simple or with 1-2 appendages. The foot is holopod. These obligatory predators are oviparous.

#### 1. Superfamily Testacelloidea

(Spiraxidae Baker, 1955; Oleacinidae Adams, 1855;  
Testacellidae Gray, 1840)

#### 2. Superfamily Streptaxoidea

(Streptaxidae Gray, 1860)

### Suborder Pupillina Schileyko, new

The shell is bulimuloid, rarely depressed or microhelicoid with columellar lamellae. The parietal lamellae are characteristic and the aperture often has parietal teeth. Female genitalia are without appendages and the penis primarily has a caecum and appendix consisting of 5 sections. The foot is holopod. With the exception of the Sagdoidea, there are no obligatory predators in the suborder. Oviparous, very rarely ovoviviparous.

#### 1. Superfamily Cerioidea

(Ceriidae Fleming, 1818)

#### 2. Superfamily Achatinelloidea

(Dendropupidae Wenz, 1938; Achatinellidae Gulick, 1873;  
Orculidae Pilsbry, 1918)

#### 3. Superfamily Cionelloidea

(Amastridae Pilsbry, 1911, Cionellidae Clessin, 1879)

#### 4. Superfamily Pupilloidea

(Pupillidae Turton, 1831; Buliminidae Clessin, 1879;  
Chondrinidae Steenberg, 1925; Pyramidulidae Wenz, 1923;  
Valloniidae Morse, 1864; Vertiginidae Fitzinger, 1833;  
Strobilopsidae Pilsbry, 1918)

#### 5. Superfamily Sagdoidea

(Thysanophoridae Pilsbry, 1926; Sagdidae Pilsbry, 1895)

#### Suborder Helixina Schileyko, new

The shell is flat to turbate, often thin and translucent and without columellar lamellae. There are no longitudinal parietal lamellae and the apertural margin is simple or with teeth. The female portion of the genitalia and/or the atrium primarily bears variable appendages or is provided with a perivaginal gland. The penis has a flagellum; there are often other appendages on the male genitalia. The kidney is shortened, the primary urethra is closed, the secondary urethra is either completely or partially closed. The foot is holopod or aulacopod. Together with herbivores there are some obligatory predators. Oviparous or ovoviviparous.

#### Infraorder Endodontinia Schileyko, new

The shell is depressed with a wide umbilicus and often with strong radial sculpture. The aperture often has teeth. The genitalia are simple with a more or less elongate vagina, at times with a glandular section. The penial papillae are absent. The foot is holopod or aulacopod.

1. Superfamily Punctoidea

(Endodontidae Pilsbry, 1894; Polygyridae Pilsbry, 1895;  
Helicodiscidae Pilsbry, 1927; Punctidae Morse, 1864;  
Pleurodiscidae Wenz, 1923; Systrophiidae Thiele, 1926)

2. Superfamily Thyrophorelloidea

(Thyrophorellidae Girard, 1895)

Infraorder Helixinia Schileyko, new

The shell is flat to spherical with the umbilicus narrowed to varying degrees. Radial rib-like sculpture on shell is exceptional and apertural teeth are rare. The genitalia are complicated with a perivaginal gland, sarcobellum, stylophores, or mucous glands with the latter usually connected to the stylophores or the sarcobellum. Penial papillae are generally present. The foot is holopod or aulacopod.

1. Superfamily Gastrodontoidea

(Euconulidae H.B. Baker, 1928; Gastrodontidae Tryon, 1866;)

2. Superfamily Rhytidoidea

(Rhytididae Pilsbry, 1893; Haplotrematidae H.B. Baker, 1925;  
Chlamydephoridae Cockerell, 1935)

3. Superfamily Vitrinoidea

(Helicarionidae Bourguignat, 1888; Trochomorphidae  
Möllerendorff, 1890; Urocyclidae Simroth 1889; Ariophantidae  
Godwin-Austen, 1888; Vitrinidae Fitzinger, 1833)

4. Superfamily Arionoidea

(Otoconchidae Cockerell, 1893; Arionidae Gray, 1840;  
Phylomycidae Gray, 1847)

5. Superfamily Sphincterochiloidea  
(Sphincterochilidae Zilch, 1959)
6. Superfamily Helicodontoidea  
(Helicodontidae Hesse, 1918)
7. Superfamily Helicoidea  
(Humboldtianidae Pilsbry, 1939; Helicidae Rafinesque, 1815;  
Helminthoglyptidae Pilsbry, 1939; Bradybaenidae Pilsbry 1939;  
Corillidae Pilsbry, 1905; Oreohelicidae Pilsbry, 1939;  
Camaenidae Pilsbry, 1895; Ammonitellidae Pilsbry, 1930)
8. Superfamily Hygromioidea  
(Hygromiidae Tryon, 1866)

#### Infraorder Zonitina Schileyko, new

The shell is depressed, zonitoid, with the umbilicus narrowed to varying degrees; a clear tendency to shell reduction and slug form is present. Sculpture is weak; apertural teeth are absent. The female portion of the genitalia has a perivaginal gland or atrial gland. The penial papillae are mostly absent or closed. The foot is aulacopod.

1. Superfamily Zonitoidea  
(Zonitidae Mörch, 1864; Daudebardiidae Pilsbry, 1908)
2. Superfamily Parmacelloidea  
(Parmacellidae Gray, 1860; Milacidae Germain, 1930)

#### Suborder Limaxina Schileyko, new

The shell is represented by a plate or separate calcareous grains. The female portion of the genitalia is without appendages; the penis is

likewise without appendages though at times a short flagellum is present. The internal structure of the penis at times is very complicated. The kidney is very variable and bears a relationship to the reduction of the shell; the urethras are closed. The foot is aulacopod. These oviparous animals are herbivores or predators.

#### Infraorder Trigonochlamydia Schileyko, new

The mantle is small, most often without a hood and sharply posterior. The penis is tube-like, smooth internally; spermatophores rest on glandular pillows and their shapes do not correspond to the shape of the penis. Obligatory predators.

##### 1. Superfamily Trigonochlamydoidea

(Trigonochlamydidae Hesse, 1882)

#### Infraorder Limaxinia Schileyko, new

The mantle is well developed, with a hood most often on the anterior part of the body. The penis is elongate or sac-like and spermatophores are not present. Herbivores.

##### 1. Superfamily Limacoidea

(Boetgerillidae Van Goethem, 1972; Limacidae Rafinesque, 1815;  
Agriolimacidae Wagner, 1935)



From the data available it appears that in the Geophila there are two basic phylogenetic branches: A) shell high, with columellar (and often with parietal) lamellae; female genitalia without appendages. B) shell depressed, without columellar parietal lamellae; female genitalia show an inclination to the formation of various, at times very complicated, appendages.

The first group includes the Achatinina, Oleacinina, and Pupillina; in the second are the Helixina and Limaxina. The apportionment, however, is not into 2 but rather 5 suborders and this is clearly seen from the early diversification of the corresponding phylogenetic branches (Fig. 7).

Near the base of the first phylogenetic branch stands the Partulidae. The reasons for thus placing the family are the following: the shell is primitive, although it also has such progressive features as an absence of parietal lamellae. The kidney is orthurethral, but one can already note the differentiation into sac-like proximal and narrow distal divisions (Fig. 8B). The foot is extraordinarily archaic (see above). The sexual apparatus is also extraordinarily and primitively simple (Fig. 8V); the simplicity is not a result of the reduction of any appendages; the seminal tube (vas deferens) is not connected directly with the penis and a penial sheath is lacking. One may think that the progressive (derived) features of the Partulidae are bound up with oviparity; individuals of the Partulidae from time to time lay 1-2 relatively large eggs, the diameter of which we compare to the diameter of the aperture of the mature mollusk. It is clear that when laying eggs of such a size -- large enough to contain the developing young -- the formation of any hard structures such as dentition in the aperture would be hampering. Kondo & Burch (1972) also emphasize the antiquity of the group.

These circumstances force one to see in the Partulidae a taxon which is close to the basic common stem from which the Achatinina, Oleacinina, and Pupillina were derived. The closer phyletic association of the Partulidae especially to the Achatinina is based primarily on the sexual apparatus. This is one of the arguments for regarding the Achatinina as the most primitive suborder and not the Pupillina as is now believed.

This conclusion is confirmed by other arguments. Thus, in Achatinina, in addition to Partulidae, there occurs an intensively developing process in the formation of sigmurethry, beginning for the most part with the shortening of the kidney. Beginning mesurethry in this way is a feature of the lower Achatinina (Megalobulimidae, Strophocheilidae, etc.). There is also another way: (of evolving sigmurethry) the closing of the urethra without noticeably shortening the kidney (Antidrymaeus, Fig. 6G). Leme (1973) suggested that the Megalobulimidae, proposed by him, is one of the most primitive groups of the order, and this once again emphasizes the correctness of our view regarding the systematic and phylogenetic placement of the Achatinina. The Megalobulimidae is the ancestor of the ancient form from which the Partulidae also originated, but the Megalobulimidae is more progressive or advanced in the structure of the kidney.

One can not doubt the unity of the conchologically strongly characterized Clausilioidea, if one omits the fossil Filholiidae. But even the sinistral Filholiidae already bear, in a weakly developed form, the features specifically peculiar to the Clausiliidae: an apertural fold and a clearly defined sinulus. The similarity and the simple arrangement of the genitalia of the Clausiliidae and Urocoptidae developed convergently and independently from the Megaspiridae. If in Clausiliidae the development of the shell was by way of

strengthening the apertural armament, then in Urocoptidae it took place in a basically different manner: through the differentiation of the columellar lamellae. Moreover, the Urocoptidae is more progressive in the organization of the excretory apparatus.

The shell of the Pupillina is more advanced in general features. The following should be added. We propose the following points which diverge even more from previous schemes and generally accepted opinions: 1) the union in one superfamily of the fossil Dendropupidae, the eastern Mediterranean Orculidae, and the Hawaiian Achatinellidae; 2) the introduction into the suborder Pupillina of the Ceriidae and the superfamily Sagdoidea.

To the first of these two points the following considerations should be stated. Knight (Moore, 1960) places Dendropupidae in the Cyclophoridae together with 2 other genera. However, it is obvious that as a matter of fact Dendropupa properly belongs with the Geophila and is not related to Maturipupa and Anthracopupa. Therefore, when we speak of the Dendropupidae we have only the real Dendropupa in mind. Thus, the families Dendropupidae, Orculidae, and Achatinellidae are united by the shape of the shell and, most fundamentally, by the presence of well developed parietal lamellae running from the first whorl to the last. As for the internal features, the Orculidae and the Achatinellidae are the only Pupillina in which the variations of the copulatory apparatus can not easily be ascribed simply to a reduction of the penial appendix or the origin of small partial changes, but they bear a 'creative' character; i.e., different elements are developed; they alter the surface appearance and the internal structure, and by no means are they cast in the static mold as in the other Pupillina (cf. Cooke & Kondo, 1960; Schileyko, 1976b). Therefore, although one can not speak of

an immediate closeness, there are some reasons to place them in the same superfamily, Achatinelloidea.

As for the Ceriidae (Fig. 9), the open secondary urethra testifies to the definite primitiveness of the group; the case of the sexual apparatus is somewhat more complicated. Firstly, the presence of a diverticulum in the spermatheca is for the Pupillina much more characteristic here than for the other groups. Secondly, the support or attachment of the penial retractor muscle to the flagellum or penial appendix, (Fig.9, PA), is a rare phenomenon and occurs only in aberrant species of the higher Geophila. From this it follows that the long appendage to which the retractor in Ceriidae is fastened is apparently the rudiment or derivative of the penial appendix. If this is true, then the family must be placed in the Pupillina. If one tries to find a place for the Ceriidae outside the Pupillina, this must be only with the Achatinina. At the same time the unique Ceriidae must be separated into a monotypic superfamily, the Cerioidea.

In regard to the Sagdoidea we must say that there are two serious objections to including them in the Pupillina: the depressed shell and the sigmurethran type of excretory apparatus. Actually the depressed shell is not typical in the Pupillina; the flat shell of Hendersoniella does not prevent the association of that genus with the Urocoptidae and the cylindrical Cylindrus is associated with the Helicidae. In addition, there exists the possibility of associating the strongly flattened shell of the type of the sagdid Lacteoluna with the high shells of the Pupillina by way of the high cupola-shaped shells of the West Indian Sagda. As for excretory apparatus, one may determine that the secondary urethra in different groups is not completely closed, and the length of the kidney in the Sagdoidea

is 2-3 times longer than the pericardium and takes in almost half the roof of the mantle cavity; in other words, the Sagdoidea is not so greatly different from the other Pupillina in this respect. In this connection it is necessary to take into account the fact that all Sagdoidea are predators and such a life style always strongly stimulates the formation of sigmurethry.

At the same time the presence of a penial appendix is characteristic of the Pupillina, and moreover, only the Pupillina. Some Sagdoidea (e.g. Lacteoluna) have an appendix of sufficiently typical structure (Pilsbry, 1940).

Let us pass on to an examination of the suborder Oleacinina. This taxon, overlooking for the moment the great conchological variability of the Streptaxidae, has a sufficiently characteristic shell and a spiral columellar lamella.

Here it is necessary to digress and once again strongly emphasize the fact that if we take into account all modifications of shell shape (in this case for the Streptaxidae), it would be impossible to establish a differential diagnosis for most families or for that matter the majority of the genera of the Geophila, not to mention taxa of higher rank. Therefore, schematic generalization is always unavoidable. When one mentions the name of any taxon there appears in the mind of the reader not some kind of definite picture, but rather a sort of generalized image of a shell shape which nevertheless contains most of the characteristic features of the taxon as a whole. Such a generalized picture nevertheless presents a very real idea of the group. We had such considerations in mind when we added figures of the shells in Figure 7.

Let us return to the examination of the Oleacinina. This suborder, in spite of all the variations of the shell, is quite compact. The repro-

ductive systems of the Spiraxidae and the Streptaxidae do not differ greatly and the chitinous hooks which occur inside the penis in several Streptaxidae are doubtlessly later derived acquisitions.

The generally simple structure of the distal portions of the sexual system is characteristic for all Oleacinina. The only complication in the Oleacinidae, for instance, is the presence of one -- rarely two -- sac-like growths on the penis (Fig. 10); in some of the Streptaxidae a penial appendage may also be present.

Let us proceed to the higher suborders --Helixina and Limaxina. First of all we must point to the widely held erroneous opinion that the Helicidae -- more definitely the genus Helix --represents the highest development of the Geophila. The slugs without doubt are the biologically most progressive shell-bearing mollusks, since the shell itself is a hindrance to biological advance, because any external stimulus brings forth a single stereotyped reaction: the animal pulls back into the shell. The mollusks without a shell must move more rapidly and possess a certain level of neural organization in order to react adequately to any kind of stimulus. Such was shown by Zs.-Nagy & Sakharov (1970) who found a much stronger development of the web of synapses in the procerebrum of Limax than in Helix. This is further exhibited in the fact that in many slugs or semi-slugs there is a tripartite division of the sole which insures a greater speed of movement. Of course, this does not mean that such a sole is a necessary diagnostic feature of this group.

In Fig. 7, the infraorder Endodontinia is treated like the main (stem) group in relationship to the other Helixina. This treatment is supported by the following facts and considerations. The shell of the Endodontidae and related groups is little specialized and may be regarded as the origin of

almost all the conchological types of the higher Geophila. The foot is holopod, the kidney sigmurethran, although in several Helicoidea the secondary urethra may be partially or completely closed (Schileyko, 1976a; Wurtz, 1955). The sexual apparatus has a primary simple structure, and it is precisely on account of that low level of specialization that the ancient Endodontinia proved to be so plastic that they provided the origin of the phylogenetic branch of the three infraorders here delineated. The basic directions of specialization may be characterized as follows:

1. A tendency to decreasing the parameters of the shell, seen for the most part in the groups from the temperate latitudes of both hemispheres (the Punctidae and the Helicodiscidae) together with the retention of a simple sexual apparatus.

2. The complication of the apertural margin because of the formation of dental armature (the Polygyridae and certain specialized tropical Endodontidae). The erection of this taxon is not correlated with any complication of the sexual apparatus.

3. The gradual reduction of the shell with a parallel significant complication of the male and female genitalia. This tendency can be seen in the many Helixina (the Gastrodontoidea and the Vitrimoidea). In other instances the reduction of the shell is not accompanied with any significant complication of the genitalia (most Zonitina).

There are three small groups related to the ancient Punctoidea whose precise systematic position is still problematic. First there is the monotypic family Thyrophorellidae. The sole genus of the family with its unique sinistral shell has the upper part of the aperture strongly projecting anteriorly and this part is semi-moveable attached to the rest of the shell.

The genitalia cast no light on the provenance of this group because of their simple structure; the only feature which is worthy of attention is the long, slightly fusiform vagina which is characteristic for many lower Endodontinia. Boettger (1962) suggested that this group should be associated with the Ario-phantoidea (i.e., in our opinion, Vitrinoidea); however, the complicated organization of the sexual system of the latter is characteristic, and we, therefore, follow Thiele (1931) and prefer to place the Thyrophorellidae in the Endodontinia, establishing for it a separate superfamily to emphasize its uniqueness.

The second group of debatable systematic placement is the Pleurodiscidae. At present the family is unanimously placed with the lower Orthurethra (essentially the Pupillina) for the reason that in Pleurodiscus both urethras are open. However, this feature should not serve as a criterion for such a high taxonomic level. The simplicity of the genitalia of Pleurodiscus is primary although such a reduction of the complicated characteristics of the Pupillina, aside from the specialized Vertiginidae, does not attain the state of terminal attachment for the sexual retractor muscle as occurs in Pleurodiscus; this feature is quite characteristic for many Endodontinia. As for the shell, it is of the type near the one which is conceivably original for the Helixina. All the non-bulimuloid shells of the Pupillina have a diameter not greater than 3-4 mm for reasons discussed above. At the same time the shell of Pleurodiscus reaches 15 mm in width. Finally it is not out of place here to put the question: what in general associates Pleurodiscus with the Pupillina aside from the formal resemblance in the structure of the renopericardial complex? One can only answer this question: nothing.



From these reasons we consider the family to be one of the lowest members of the suborder Helixina which retained the orthurethran type of excretory apparatus.

A third familial group questionably included in the Endodontinia is the Systrophiidae. The shell has a typical endodontid appearance. The sexual system lacks appendages and an epiphallus is not marked. Characteristic is the terminal attachment of the sexual retractor muscle; in other words, the Systrophiidae are typical members of Endodontinia. Nevertheless they are always associated with the typically predatory families (the Zonitidae and the Trigonochlamydidae). However, the predatory specialization takes place in various taxa of the Geophila, and one can observe its independent origin in several lineages. The Endodontinia constitute no exception. Naturally the change to the predatory condition is accompanied by corresponding changes in the structure of the radula, foot, and renopericardial complex.

Solem (1975) has convincingly shown that the Helicodiscidae should be an independent family.

Among the Helixinia the only obligatory predators are the Rhytidoidea reflected also in their outer appearance. Further, this is also one of the rare cases when the predator has a non-aulacopod foot. Nevertheless the character of the mobility of these animals deserves a thorough investigation. (cf. supra, Fig. 3, VI-VII).

In Fig. 7 it is seen that the Euconulidae and the Gastrodontidae are removed from the Zonitidae and associated as the Gastrodontoidea with the Vitrinoidea. Their removal from the Zonitidae was explained earlier (Schileyko, 1972a). There are no serious objections to the placement of these families

near the Vitriinoidea (Van Mol and Van Bruggen, 1971; Verdcourt, 1960). Moreover, the association of the Helicarionidae with the Vitriinoidea is confirmed by the fact that in the Vitrinid genus Semilimax there is a sarco-belum of characteristic structure (Hubendick, 1953 and our own data).

The organization and the phylogeny of the higher Helixinia --Helicoidea of authors -- has already been considered (Shileyko, 1978). Therefore, we will confine ourselves to the main points here. Basically it must be emphasized that it is impossible to associate the Helicoidea and the Hygromioidea to one another on anything but superfamilial grounds. Thus, if we were to take the most archaic groups among these taxa, namely the Humboldtianidae and Trichiinae, we would discover two distinctly different methods of the placement of the stylophores (Vide supra). There is another sharp difference between these superfamilies: in the Helicoidea, the reservoir of the spermatheca is connected by bodies of connective tissue to the bottom of the mantle cavity and presses into the base of the albumen gland: in the Hygromioidea the spermatheca is not bound up with the mantle cavity but is joined to the spermoviduct.

The Helicodontoidea apparently is a heterogenous group and at present it is difficult to determine its phylogenetic connections. One may only note that there are four types of sexual systems (Helicondonta, Lindholmiola, Oestophora, and Mastigophallus) whose phyletic succession cannot be traced. The shell alone unites them in one superfamily -- flat, multi-whorled, with reflected apertural margins.

The organization of the Sphincterochilidae has been discussed often (Shileyko, 1972b; Forcart, 1972a, b); the unique structure of the foot and the sexual apparatus has been emphasized as reflecting a considerable

distinction of the family from other helicoid groups. At the same time the association of the Sphincterochilidae with the Helicoidea is not in doubt. This is due most of all to the typically helicoid shell of Sphincterochilidae which only too clearly relates the group to the Helicoidea. Nevertheless, if one were to disassociate oneself from the prejudice exerted by external appearance and compare the sexual system of the Sphincterochilidae with the genitalia of the Vitrimoidea, it is not difficult to see how the Sphincterochilidae naturally fits into a scheme more closely related to vitrinoids than to the helicoids; the sarcobelum is armed with a mucous gland; the penis has a sac-like appendage and a flagellum (cf. Solem, 1960; Van Mol, 1968, 1970, 1973). The low degree of specialization of the sexual apparatus in the Sphincterochilidae forces one to see it as a group close to the ancestral form of the Vitrimoidea though still noticeably divergent. In the Vitrimoidea, the tendency to shell reduction is characteristic. The higher members of the superfamily are already slugs or semi-slugs. The lower Vitrimoidea have well developed shells, and the ancestors of Sphincterochilidae, possessing a normal shell, adapted to living in arid conditions; their development was directed toward the thickening of the shell walls and the formation of other adaptive features (i.e. white color and sharply narrowed aperture).

The infraorder Zonitina derived independently from the Helixina from ancient Endodontina and are clearly separable into two superfamilies: 1) Zonitoidea, in which the process of shell loss can be observed as the lineage turns predatory; and 2) the Parmacelloidea which completely or partially loses the shell in going from herbivorous to omnivorous.

The peculiarities of the organization of the suborder Limaxina,

composed exclusively of shell-less forms, has been discussed by Likharev & Victor (1979).

In summary, in examining the evolutionary paths in the suborders and infraorders, one may note the following lines of specialization and development of different organs and structures which appeared independently and convergently in all taxa.

1. The appearance of sigmurethry with complete closing of the urethra.
2. The formation of the aulacopod foot often accompanied by the appearance of a tripartite sole.
3. The reduction of the shell and the evolution of the slug form.
4. The transition to a predatory state; this process was often associated with the elaboration of a higher direction of specialization.

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Fig. 1 Comparative shell volume occupied by the molluscan body (darkened) in regard to the extent of the umbilicus. The shells have the same proportions and the same contours.

A. Widely umbilicate B. narrowly umbilicate.

Fig. 2 The types of placement of the grooves in the foot of the Geophila.

- I) from under the buccal flap extend a few short suprapedal grooves (Partula)
- II) the same type (Placostylus, Helicophanta, Urocontidae)
- III) only peripedal grooves (Cerion, Oleacina, Paryphanta, Helix, Subulinidae, Clausiliidae)
- IV) suprapedal and peripedal grooves (sic) (the author means with one pair of pedal grooves and one pair of suprapedal grooves (Nesovitrea and Ceciloides))
- V) two pairs of suprapedal and one pair of pedal grooves. (Macrochlamys, Vitrina, Oxychilus, Trigonochlamys, Limax)
- VI) one central pedal groove (Rhytida)
- VII) one central pedal groove and a pair of suprapedal grooves (Zonitoides)
- VIII) a pair of suprapedal grooves (Vitrea)
- IX) two pairs of suprapedal grooves (Discus, Arion)
- X) groove absent, but waves of locomotor contractions pass only along the central part of the sole (Achatina)
- XI) hypothetical variant of the appearance of pedal grooves at the expense of the differentiation of the central field.

Incisions in II-XI made on the level indicated by dashed line in I.





Figure 1

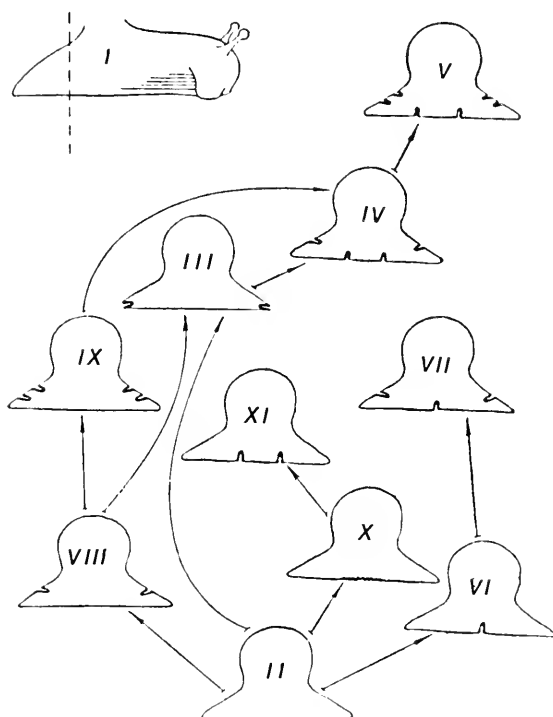


Figure 2





Fig. 3. Two methods of flagellum formation

- I-IV) The descent of the seminal duct (vas deferens) distally.  
V-VIII) The junction of the lower end of the seminal duct (vas-  
deferens) with the apical part of the epiphallus.

Fig. 4. Schematic representation of the male sexual section of Pupillina.

A1-A5 - parts of the penial appendix

PR - sexual or penial retractor muscle

F - flagellum

C - caecum



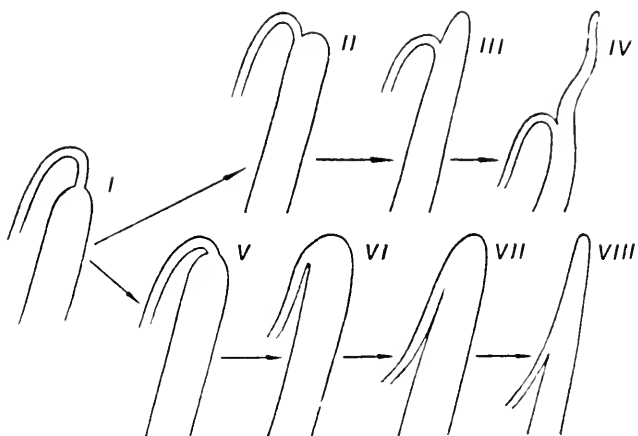


Figure 3

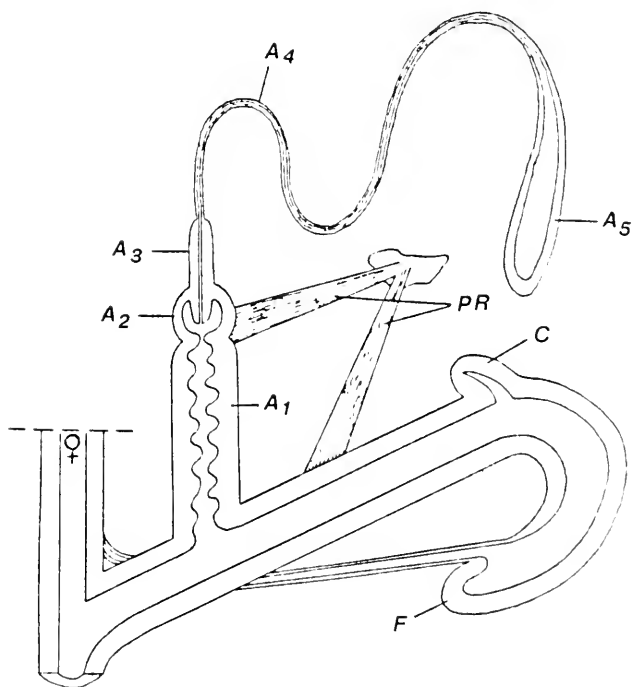


Figure 4



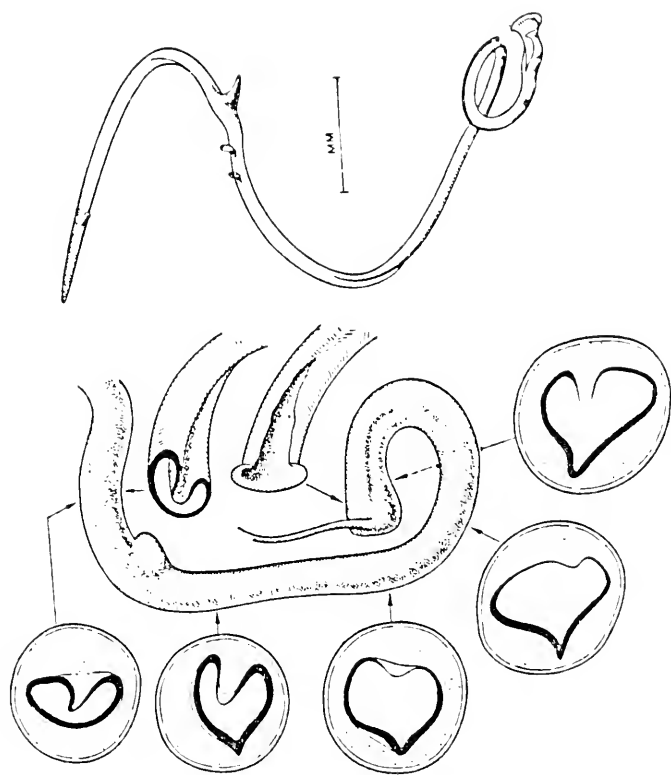


Fig. 5. External view and form of the spermatophore in Pseudonapaeus albiglicatus (Mts.) (Pupillina, Buliminidae) above -- a spermatophore taken from the spermatheca; below -- the epiphallus and cross section through the "tail" of the spermatophore. The walls of the spermatophore shown in sections.



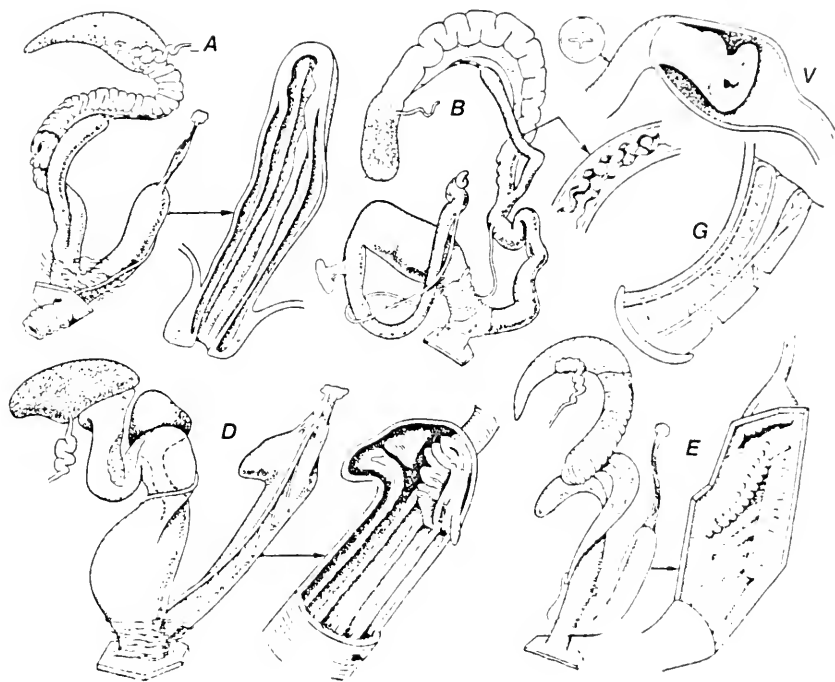


Fig. 6. The reproductive system and its structural details in different Achatinina.

A - Placostylus shongi (Less.) from New Zealand (Bulimulidae); the reproductive system and with penis opened

B - Antidrymaeus inusitatus (Fult.) from Brazil (Orthalicidae); (Orthalicidae not separated from Bulimulidae) the reproductive system and the partially opened spermatheca

V - the same with the penis opened

G - the same showing the organs of the mantle cavity

D - Helicophanta magnifica (Fer.) from Madagascar (Acavidae); the reproductive apparatus and the opened penis

E - Rumina decollata (L.) from Algeria (Subulinidae); with the reproductive apparatus and the opened penis









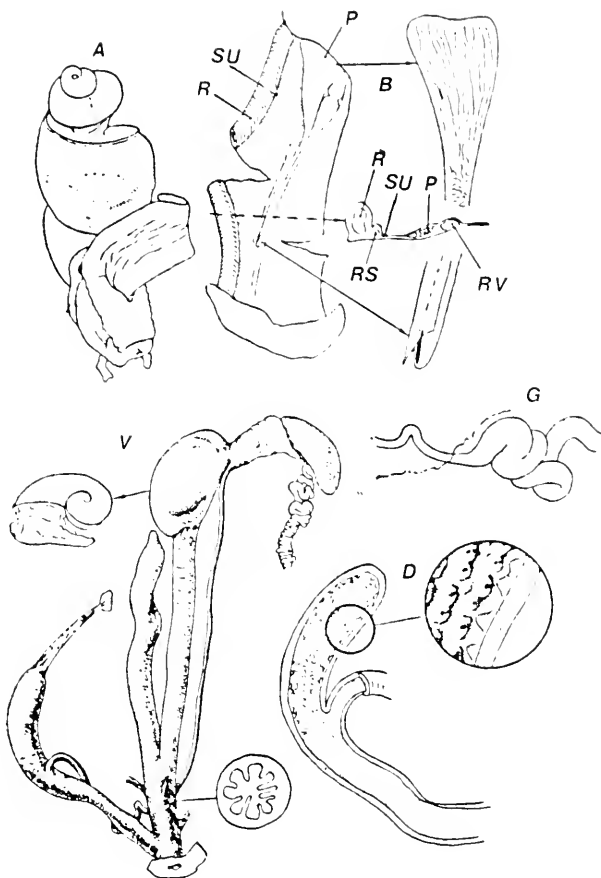


Fig. 8. Partula otaheitana (Brug.) from Tahiti, Tahiti-nua.

A - external view of the soft parts taken from the shell

B - organs of the mantle cavity

V - reproductive system

G - part of the hermaphroditic duct and quadrivium or fertilization chamber

D - penis opened

SU - secondary urethra

RV - respiratory vein

K - kidney

R - rectum

RS - rectal sinus



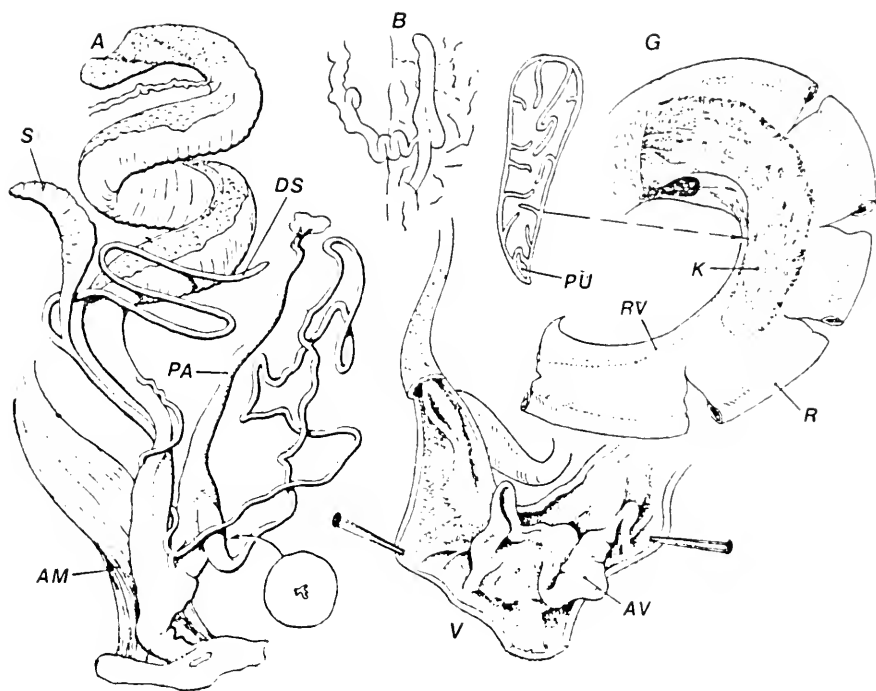


Fig. 9. Cerion glans (Kust.) from Cuba.

- A - reproductive apparatus
- B - quadrivia or fertilization chamber
- V - atrial section of the genitalia
- G - roof of the mantle cavity and cross section of the kidney
- PA - penial appendix
- AV - atrial valve
- AM - atrial muscle
- DS - diverticula of the spermatheca
- RV - respiratory vein
- K - kidney
- PU - primary urethra
- R - rectum
- S - spermatheca



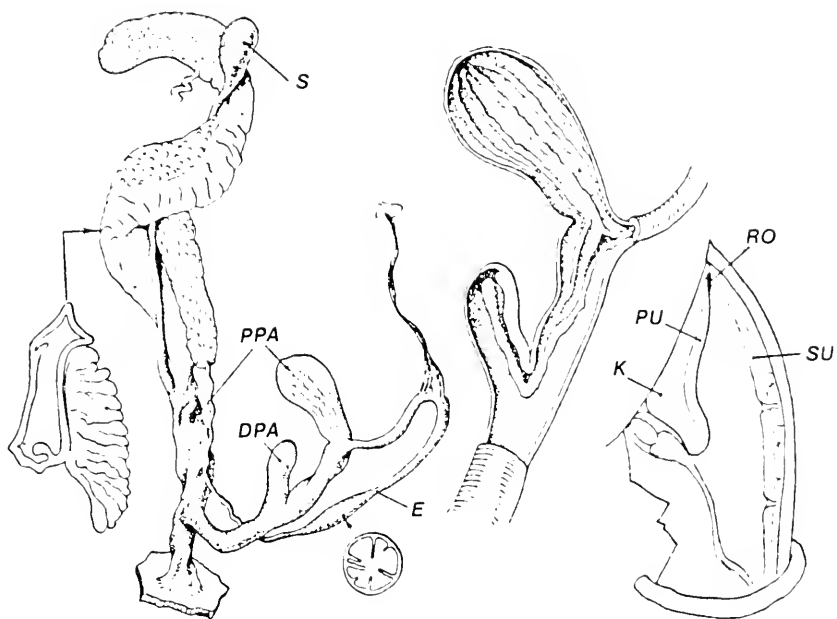


Fig. 10. Oleacina solidula (Pfr.) from Cuba. Left - reproductive system and cross sections through uterus and vas deferens. Center - penis in the region of its appendages, opened. Right - organs of the mantle cavity.

DPA - distal penial appendage

PPA - proximal penial appendage

SU - secondary urethra

K - kidney

PU - primary urethra

RO - renal orifice (orifice of primary urethra)

S - spermatheca

E - epiphallus













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